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ECOLOGY, SELECTION AND SYSTEMATICS

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ABSTRACT. Three different kinds of ecological relationships between newly separated species are examined, with the aim of establishing their expected effects on the systematic differences between the species involved. In cases of slight difference between the habitats of two products of recent speciation, selection can be expected to favor specific competitive mechanisms, but taxonomic differences would be expected to be slight, and examples of hybrid superiority would be common. Where the habitats of the two species are markedly different, as along a steep ecological gradient, adaptation to the different places will result in species that become broadly overlapping in habitat, and taxonomically different in many clearly adaptive characters. Although this latter process leads to species with somewhat different food habits, it would not lead to food specialization, even if the two species were originally limited in abundance by food and in competition for it. True food specialization, in the form of monophagy, is most likely to evolve in the presence of a superabundance of several kinds of food, owing to increased efficiency of handling, digestion and metabolism, and is improbable among species in competition for food. Closely related monophagous species should differ markedly in a few characters, and hybrids should be inferior. Examples of the three situations are described, plethodontid salamanders being used for the first two and leaf-mining insects for the third.

INTRODUCTION

Classically, the relationship between systematics and ecology has been approached by first taking systematics as the exploration of genomic diversity, and then turning to ecology for explanations that were secondary to the origin of differences. This approach is epitomized by the recent comment to me that the reproductively isolated entities within *Paramecium aurelia* could

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now be considered species because their isoenzyme patterns are visibly different. Such a viewpoint surely gets the classification much too far away from the biology. As an antidote, I propose to examine the relationship from the standpoint that ecology provides the set of opportunities that can be exploited by diversification of the genome. The approach is not original, as it is the basis for the idea of adaptive radiation, but the impact of ecology on systematics deserves reexamination. In this, we should separate the passive background from the active; that is, those factors that set the conditions, and those that are able and likely to respond by evolving themselves. These two classes, unfortunately, will not remain constant for us. For example, it would be agreed that the distinction between nonliving and living parts of the environment might provide such a preliminary classification, but as far as I can discover, this is not the case. The distinction between the vegetation on one hand and the climate and substrate on the other is clear enough. The physical gradients provide the passive background, making physiological demands on a potential additional plant species, and the various competing species of plants provide the active counteradapting background, making ecological demands.

However, when we consider the active and passive background of animals, particularly carnivorous ones, the distinction between plants and the physical environment becomes less important than the distinction between both of those on the one hand and other animals on the other. Indeed, there are few cases of terrestrial predators which are distributed concordantly with even the dominant plants, and when this coincidence does occur, the plants are used in a nonliving context, as when they are required for nest sites.

This example provides the opportunity to emphasize the distinction between selection for physiological adaptation and selection in response to the ecological pressures of competition and predation. It is to the latter to which I wish to address myself principally, but I first give an example of the simultaneous operation of both. This will be followed by a description of what seems to me to be an unusual opportunity to investigate the ecological interaction between one species and several geographically varying populations of another, closely related one. From that, I hope to be able to generalize some about a fruitful investigation of other kinds of systematic consequences of ecological phenomena.

AN ANALYSIS OF THE EXPLOITATION OF A UNDIMENSIONAL GRADIENT

As has been emphasized by Dunn (1926), (Hairston, 1949), Organ (1961) and others, the evolution of the Dusky Salamanders of the genera *Desmognathus* and *Leurognathus* is describable in terms of adaptation to a linear series of habitats from aquatic to terrestrial.

This unidimensional array of pertinent physical environments facilitates the analysis of each species' most immediate biological environment: namely, its closest relatives.

My own early analysis showed that the coexistence of five species was possible, when they used the entire physical gradient from completely aquatic to terrestrial. The species involved are *Leurognathus marmorata*, *Desmognathus quadramaculatus*, *D. monticola*, *D. ochrophaeus* and *D. wrighti*. The distribution of the four species of *Desmognathus* is shown in Figure 1. With no further information, however, it was not possible to determine whether more species could be accommodated in this presumably competitive series.

Some years later, Organ was able to provide a tentatively negative answer when he investigated the ecological distribution of the same four species of *Desmognathus* in an area where a fifth species, *D. fuscus*, was found. He found that at nearly every location, the maximum number of species present was four. *D. fuscus* could coexist either with *D. quadramaculatus* at high elevations or with *D. monticola* away from large streams at lower elevations but not with both.

Thus, the limit imposed by the presumably competitive relationships seems to have been reasonably well established, but a more detailed look at the data suggests that steepening of the moisture gradient may reduce the number of species that can be accommodated from the competitive standpoint. At high elevations, atmospheric moisture, however expressed, is as great far from water as it is over a stream at low elevations (Hairston, 1949). This correlates very well with the combined vertical and horizontal distributions of the two most terrestrial salamanders, *Desmognathus ochrophaeus* and *D. wrighti*. *D. ochrophaeus* is confined to a zone near streams at low elevations, none having been found more than 15 feet from a stream at elevations below 3000', but its distribution is unrelated to surface water above 4500 feet. *D. wrighti*, with its distribution unrelated to water in summer, apparently cannot compete with its congeners close

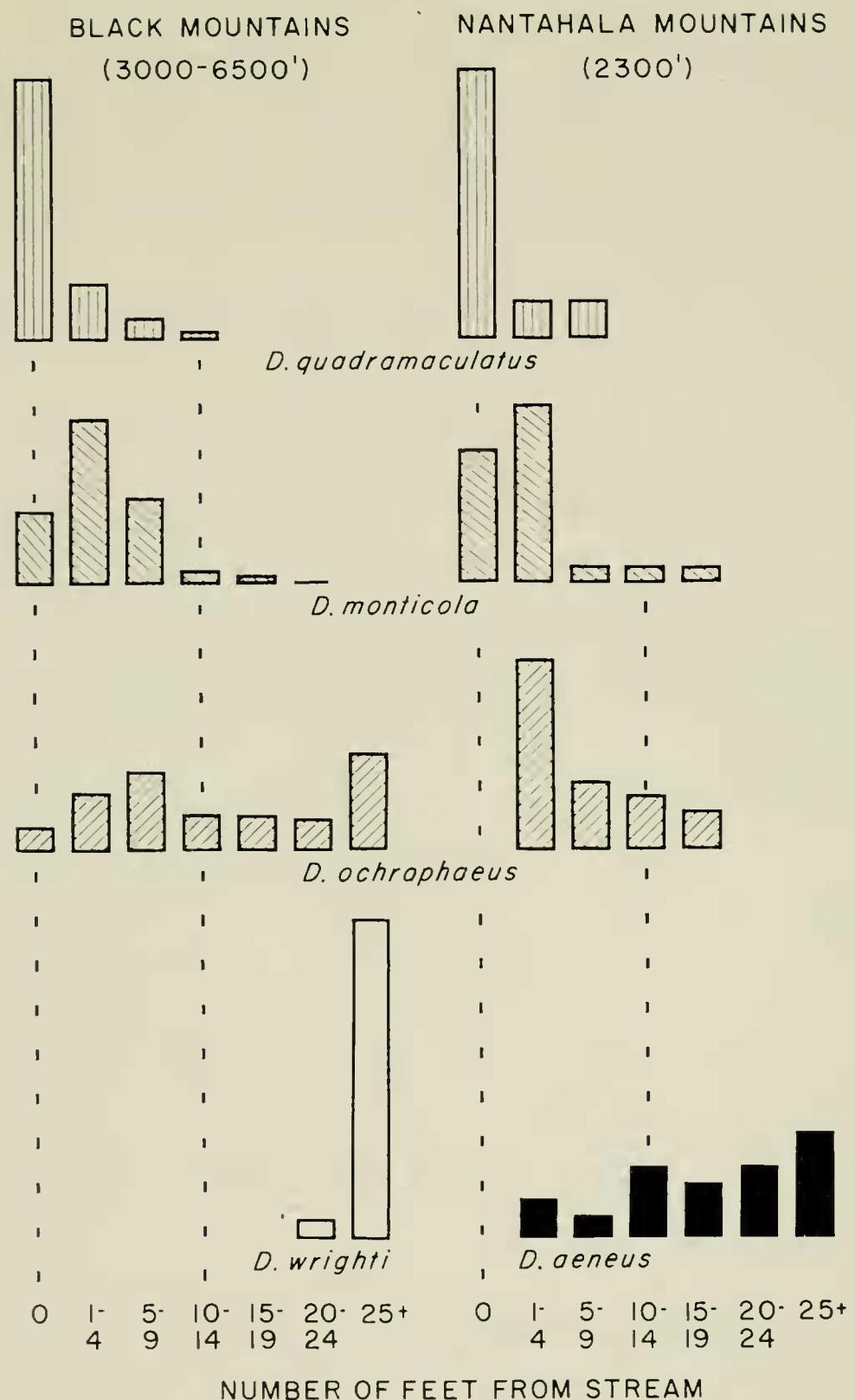
DISTRIBUTION OF *DESMOGNATHUS*

Figure 1. The ecological distribution of the species of the salamander genus *Desmognathus* in two different mountain ranges in North Carolina.

to streams at low elevations, and cannot persist away from streams there because of the lower moisture.

It is therefore with some interest that one notes the coexistence of four species of *Desmognathus* at low elevations (down to 2200 feet) in the Nantahala Mountains. *D. wrighti* does not occur at low elevations, but a study of the ecological distribution of the genus shows the presence of a terrestrial species, *D. aeneus*. This species, which is the size of *D. wrighti*, but more slender, was found closer to streams than *wrighti* usually is in summer, but clearly occupies the same general position at the terrestrial end of the environmental gradient (Fig. 1). It seems anomalous that it should be present, although *D. wrighti* is unable to occupy the corresponding habitat at low elevations near its range. It was postulated above that this inability is related to reduced moisture at low elevations. This suggests that there may be a climatic variation that permits the existence of a low-altitude terrestrial *Desmognathus* in the Nantahala Mountains. An examination of rainfall records reveals that such is the case. In the Coweeta Experimental Forest, the location of the distributional study, the average annual rainfall ranges from 75 inches at 2240 feet to 93 inches at 3870 feet. This is appreciably higher than the rainfall at comparable elevations elsewhere in the Southern Appalachians. For example, at the foot of the Great Smoky Mountains, Bryson City, N.C. has an average annual rainfall of 52.12 inches. At the foot of the Black Mountains, Montreat and North Fork have 53.61 and 51.78 inches respectively, and between the Smokies and the Blacks, the French Broad Valley receives from 38.45 inches at Enka to 47.61 at the Asheville-Hendersonville Airport.

Among other locations at comparable elevations in the Southern Appalachians, only the region from Brevard to Highlands, N.C. receives as much rain as the general area south and west of the Little Tennessee River. Comparable rainfall is found elsewhere only at high elevations (71.20 inches at Mt. Mitchell, 6684' in the Black Mountains, and 81.71 inches at Clingman's Dome, 6643' in the Great Smoky Mountains).

The end of the series of species seems to be determined by climate, with high rainfall permitting the addition of a small terrestrial species. On larger and higher mountains, when the tops are (or once were) covered with conifer forests and rainfall is high, the terrestrial species is *Desmognathus wrighti*, which is confined to elevations above 3500 feet; in that part of the mountains where the rainfall is high, even at low elevations, *Des-*

mognathus aeneus occupies the terrestrial end of the series. In other areas, the series stops with the third species, *D. ochrophaeus*. It does not appear possible for another species to enter the series in the middle, as shown by the situation with *D. fuscus* at White Top Mountain in Virginia. Competition thus seems to determine how similar any pair of species can be and still coexist. When the climate would require the next most terrestrial species to overlap the habitat of *D. ochrophaeus* to too great an extent, only three species are found.

This situation seems to present an unusually clear example of the evolutionary exploitation of a simple environmental gradient and of the limits of this diversifying exploitation that are set by competitive interactions. The limits to "species packing" are demonstrated as clearly as post-facto analysis could permit.

Moreover, it provides a miniature model for the early stages in the evolution and diversification of the family Plethodontidae.

POST-SPECIATIONAL EVENTS: INCREASED COMPETITION OR COEXISTENCE?

The kind of analysis made in the preceding section differs from large numbers of published descriptions only in being a little more tidy than most. If the field is to progress, such statements will become the beginning of studies at the interface of ecology and systematics, rather than representing final conclusions. The choice among investigations of ecological distribution should depend upon the respective opportunities that they present for experimental tests of hypotheses of systematic status or ecological processes. One of the points which I wish to make most strongly is that experimentation related to ecological interactions can yield important information about evolutionary events, provided that care is taken to select appropriately favorable situations for study. One such situation that seems to be especially suitable for field manipulations is represented by two species of *Plethodon*, an exclusively terrestrial genus of salamanders. The location is also the Southern Appalachians.

Plethodon jordani is endemic to the southern Appalachians. Through much of its range, it is confined to higher elevations, resulting in a fragmented distribution consisting of a number of isolated populations, many of which are morphologically distinct from each other. These populations have been studied repeatedly, and have been classified as belonging to as many as four distinct species (Grobman, 1944). Whenever specimens

have been taken from intermediate locations, they are intermediate in color between the adjacent different populations. This discovery led to the eventual inclusion of all of these populations within *Plethodon jordani* and the recognition of seven subspecies (Hairston and Pope, 1948; Hairston, 1950). The subspecies are no longer recognized, largely because at least some of the color characters are distributed independently of one another. The situation as it is presently known is described by Highton (1970, 1971) and by Highton and Henry (1970), who add the electrophoretic patterns of plasmaproteins to the characters for which distributional data are available.

Plethodon glutinosus is widespread throughout the eastern United States. In the Southern Appalachians, it tends to occur at lower elevations than those at which *P. jordani* does, and I have suggested that the sharp altitudinal replacement of the two species is the result of competitive exclusion (Hairston, 1949, 1951). Although easily recognizable color differences are known for at least four geographically distinct parts of the *P. glutinosus* population (Highton, 1962, 1970, 1971), the population in the area discussed herein consists of only one of these. *P. glutinosus* is thus morphologically more uniform than is *P. jordani*. The above-mentioned altitudinal separation of the two species is not the case everywhere, however. Over the southeastern part of the range of *P. jordani*, the two species occur together over nearly the entire range of altitudes available, indicating that competition does not play a significant role in their distributions. This observation, reported by me for a few vertical transects (Hairston, 1951) has been confirmed and extended by Highton. The fact that in this area *P. jordani* occurs at lower elevations and *P. glutinosus* at higher elevations than elsewhere strengthens the conclusion that in the areas of altitudinal replacement, there is intense competition in the narrow vertical zones of overlap. It is this geographical difference in ecological relationship between the two species that provides an unusual opportunity to investigate the phenomenon of competition in the field, and to obtain evidence on the sequence of evolutionary events accompanying competitive interactions between two similar species.

The above account is oversimplified from the taxonomic standpoint. Over most of the area west of the French Broad River, the two species are distinct, but Highton has found hybrids at appropriate elevations on some of the mountains, and intergradation is so extensive in the Nantahala Mountains that the local form of *P. jordani* was once described as a subspecies of *P.*

glutinosus (Bishop, 1941). Highton has called specimens from intermediate elevations a hybrid swarm. Two detailed vertical transects in the Southeastern Nantahala at Coweeta Experimental Forest show that simple explanations of the relationship are unlikely to be satisfactory. The forest has two more or less parallel roads that ascend to the top of the mountain. The roads diverge slowly from the foot of the mountain at 2200 feet, being a little more than one mile apart at 3200 feet and around two miles apart at the points where they reach the top of the ridge at 4100 and 4500 feet, respectively. In October, 1971, a transect was carried out along the more northern road, to be referred to as the Shope Creek Road. The conventional expectation would be of continuously increasing similarity to *P. jordani* and decreasing similarity to *P. glutinosus* with increasing altitude. The comparison was made on the basis of color alone, no other known character being of value in that part of the range. Four different color characters are possible. *P. jordani* is characterized by red legs and a pale belly; *P. glutinosus* has extensive white spotting, especially on the sides, and a black belly. A population of *P. jordani* 10–15 miles to the east has extensive brassy spotting on the back, as well as some white spotting on the sides, but at present seems to be distributed discontinuously from the Nantahala population. A few specimens from the transect had brassy spots, but were too few to yield meaningful information. Arbitrary scales were established to compare the relative amount of red on the legs, white spotting, and darkness of belly color. Six to 20 specimens were collected at each of 11 elevations from 2200 to 4300 feet. For each collection, an average intensity of each character was established by five different observers, and the results pooled. The three characters changed in exactly the same way along the transect. The results for two of them are shown in Figure 2. The reversal of the expected trend led to a transect of the southern road (Ball Creek) in 1972. The results, shown in Figure 3, conform to the original expectation, but do not agree with the Shope Road transect, which was repeated in 1972 with virtually identical results to those obtained in 1971 (Fig. 2).

Although the 3800-foot site is located on an east-west ridge, the same is true of all higher sites, and no obvious vegetational differences could be seen to account for the difference between the transects — impressions confirmed in the records from 69 widely dispersed rain gauges (Dils, 1957).

Whatever the eventual explanation for these anomalous data,

ALTITUDINAL VARIATION IN COLOR CHARACTERS IN *PLETHODON*
ALONG SHOPE CREEK WATERSHED

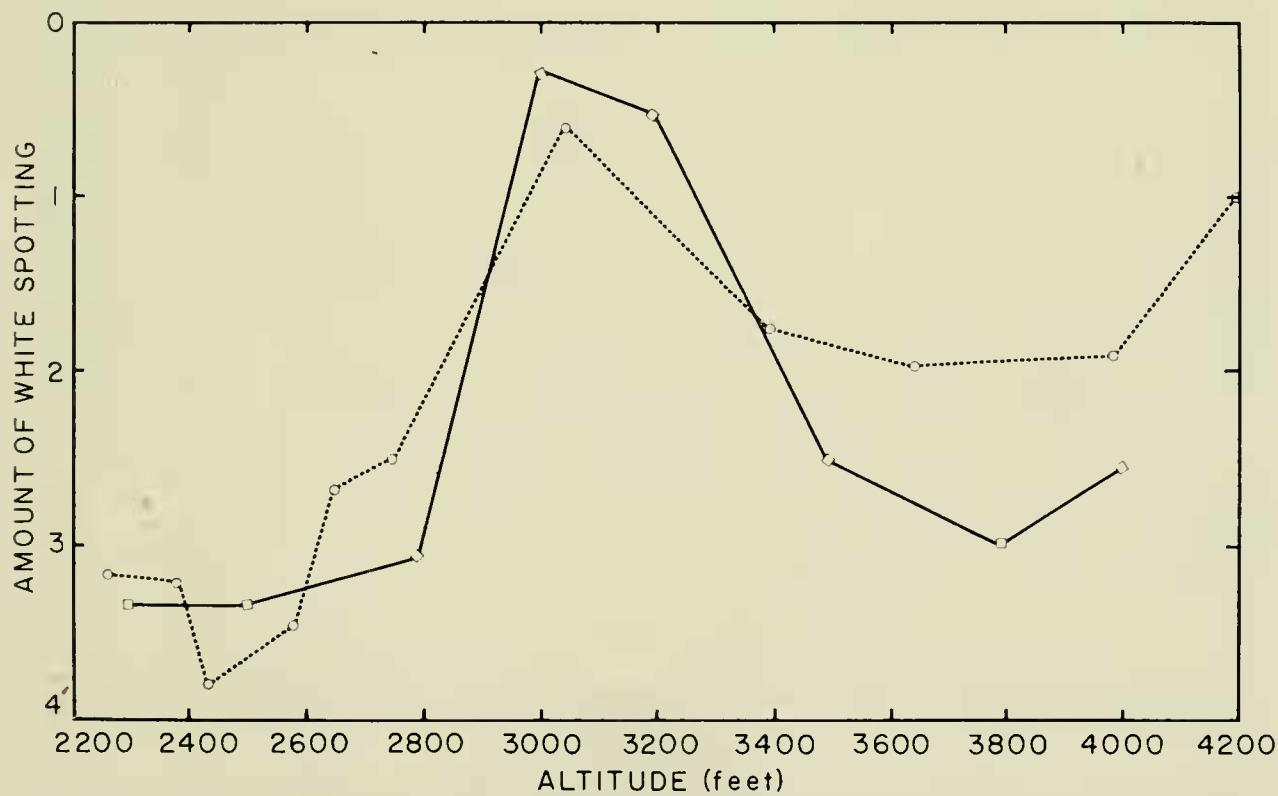
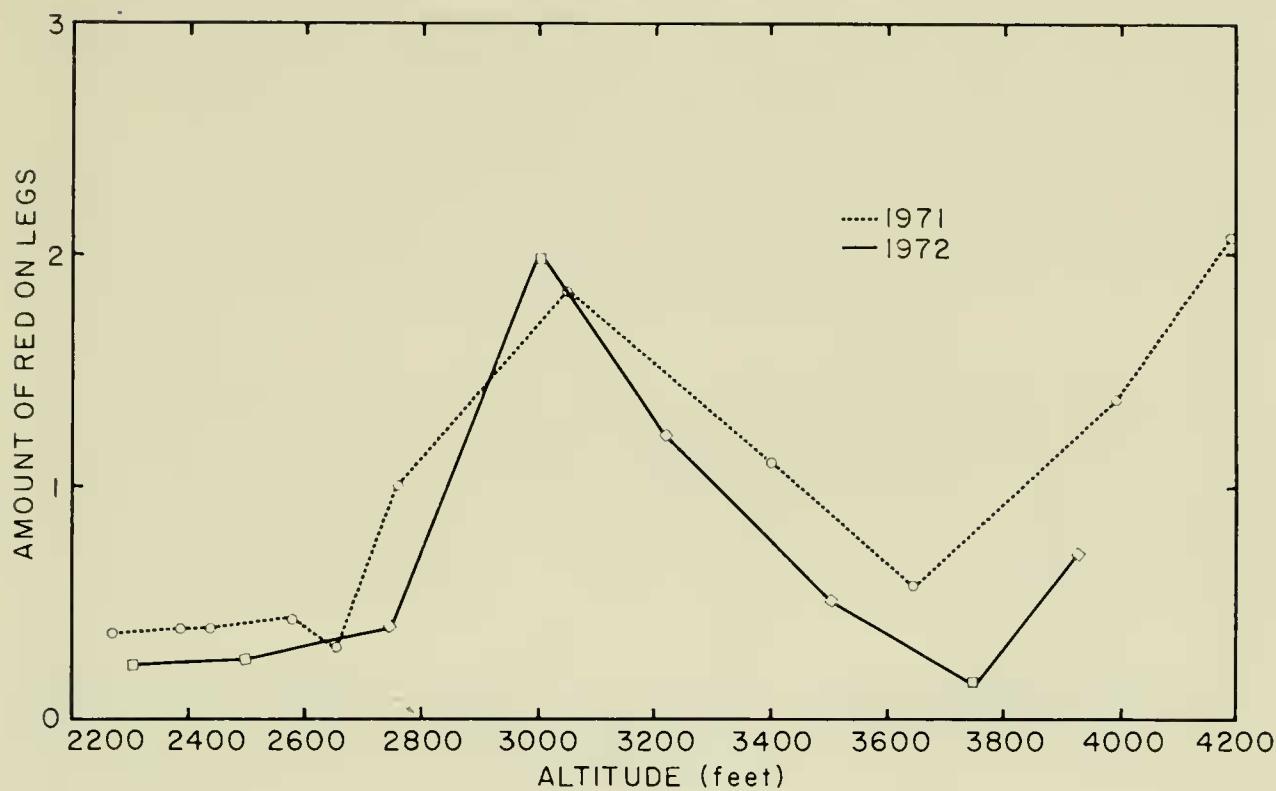


Figure 2. The vertical distribution of two color characters in the salamander genus *Plethodon* along the Shope Creek transect in the Nantahala Mountains in North Carolina. The scale for white spotting has been inverted because white spots are characteristic of the low-altitude species.

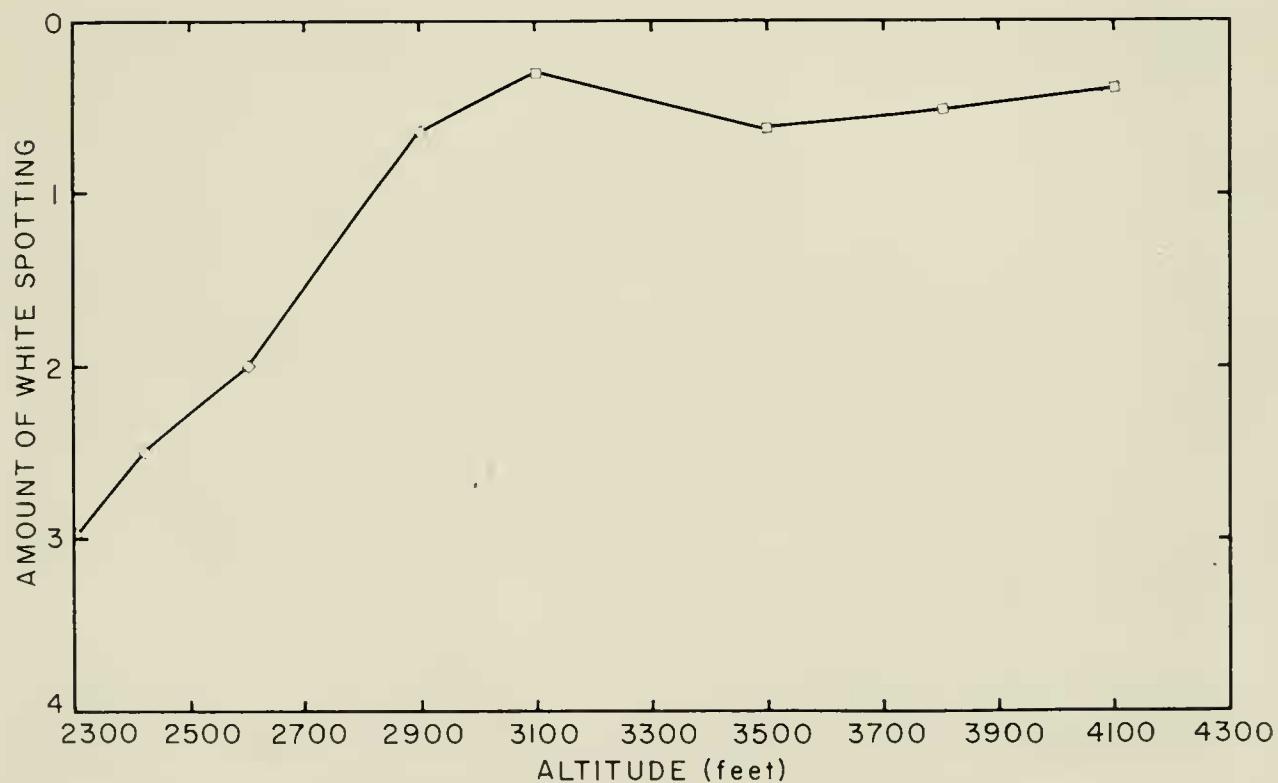
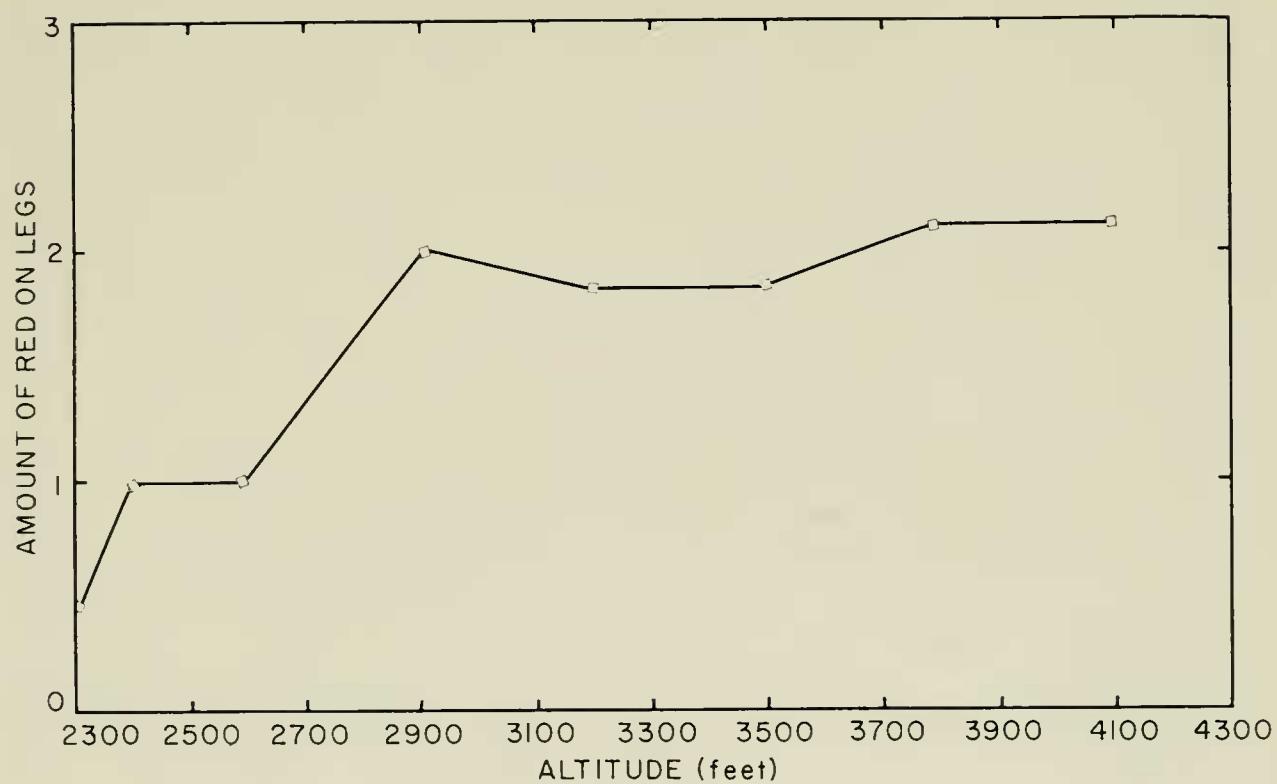
ALTITUDINAL VARIATION IN COLOR CHARACTERS IN *PLETHODON*
ALONG BALL CREEK WATERSHED

Figure 3. The vertical distribution of two color characters in *Plethodon* along the Ball Creek transect, for comparison with Figure 2.

they reflect complications in the relationship between the two species, and further investigations may reveal or at least suggest very local selective forces.

The situation in the Nantahalas gives a strong indication of close taxonomic relationship between *P. glutinosus* and *P. jordani*, and is thus useful information in suggesting ecological and especially evolutionary questions about the two species elsewhere in the Southern Appalachians where hybridization is absent or very rare.

Current evolutionary theory would explain the observed ecological distributions in these other areas in the following manner: assuming, as seems likely, that *Plethodon glutinosus* and *P. jordani* share a common ancestor in the not very remote past, the speciational event separating them left two species with adjacent geographical ranges and very similar ecological requirements. *Plethodon jordani* presumably occupied the southern part of the Blue Ridge physiographic province, and the relevant part of *P. glutinosus* occupied the adjacent part of the Piedmont province. With a warming climate, *glutinosus* has invaded the valleys of the Blue Ridge province, but competition from *jordani* has prevented *glutinosus* from extending its range to the tops of at least some of the mountains, notably the Great Smoky Mountains, the Black Mountains, and the Unicoi Mountains. Throughout most of the rest of the area of common distribution, one or both species have evolved into ecologically divergent directions, with the result that competitive exclusion no longer operates, and the two species coexist over a wide range of elevations. This situation would represent character displacement in the use of some ecological requirement as yet unidentified. In the areas of competitive exclusion, the vertical overlap of 200 feet represents the uncertainty of outcome of competition owing to climatic variability, *P. jordani* being favored by cool, wet years and *P. glutinosus* by the reverse conditions.

Thus, in conventional theory and as far as numerous observations have revealed, we have the same two species coexisting in some areas and in intense competition in others. Geographic variation in color of *P. jordani* provides independent identification of representatives from the two ecologically different populations, and this and other features make it feasible to undertake experimental manipulations to test the accuracy of the interpretations that I and others have made of the present distributions of the local populations of the two species. This should be done by reciprocal removal experiments and by exchanging numbers

of *Plethodon jordani* between the two areas of presumably different ecological relationships. Inasmuch as they differ in color pattern, the introduced individuals and their descendants would be readily identifiable for an indefinite number of years after the start of the experiments.

The most obvious first test of the interpretations would be to remove each species separately from different plots in the different areas where competition is and is not expected. If the interpretation is correct, the remaining species should show a much greater response in the area of narrow vertical overlap than in the area of wide vertical overlap.

Whatever the outcome of these simple removal experiments, they would help resolve an implicit contradiction in ecological theory. This is the conflict between the often used theory that distributional overlap between closely related species implies an appreciable amount of competition (Levins, 1968; MacArthur, 1968) and the converse that the same overlap implies that competition is reduced or absent (Crombie, 1947; Hairston, 1951; Brown and Wilson, 1956; MacArthur, 1972: 29 ff). This conflict is rarely stated overtly, but its resolution could have a profound effect on ecological theory, including much that has been written about niche breadths and community matrices.

The implications of the simple removal experiments are more directly ecological than they are evolutionary. The combination of ecological and systematic situations provides the opportunity for more sophisticated experiments whose results could yield important insights into the recent influence of natural selection on the direction of evolution in the several populations of *Plethodon jordani*. These experiments would consist of reciprocal transplants of populations of *P. jordani* between an area of narrow overlap and one of wide overlap. The subsequent changes in the transplanted *jordani* populations and in the *P. glutinosus* populations newly exposed to the foreign *jordani* would reveal the direction of recent evolution with respect to interspecific competition.

If *P. jordani* from the area of wide overlap survived in the area of narrow overlap, and the *P. glutinosus* population increased, the interpretation would be that in the area of wide overlap, *P. jordani* has evolved so as to decrease its competitive interaction with *glutinosus*. If *P. glutinosus* has evolved in the same way, the reciprocal experiment should result in no change in the *glutinosus* population, and it might result in an increase in the *jordani* population introduced from the area of narrow over-

lap, because the *jordani* would not be meeting as much competition as it had been experiencing before the experiment.

Conversely, if the *P. jordani* transplanted from the area of narrow overlap increases in the area of wide overlap at the expense of the local *P. glutinosus*, it would be necessary to conclude that recent evolutionary history had produced a specialization in *jordani* for some specific competitive mechanism.

A decrease in and eventual disappearance of *jordani* moved from the area of wide overlap, combined with an increase in the local *glutinosus*, would be interpreted to mean the evolution of a specific competitive mechanism in that population of *glutinosus*.

The complete set of possible experimental outcomes and their interpretations is given in Tables 1 and 2. Specifically omitted from the tables are the highly necessary controls. For the removal experiments, the only controls required are undisturbed plots containing both species. The reciprocal transplantation of populations of *P. jordani* will require elaborate controls. First, one must be satisfied that the salamanders can be moved at all and continue to thrive. This will require transplanting animals within an area where their ecological relationships appear to be constant. Assuming the success of such an experiment, it will also be necessary to provide assurance that they are physiologically capable of existing in the remote area where the competitive relations are presumably different. For this control, it will be necessary to first remove both species from a plot and then introduce the foreign *jordani*. Its survival would assure an interesting result on those plots where it was introduced into contact with *glutinosus*. The failure of any of these controls would of course mean that the main experiment in reciprocal transplantation of populations was a failure. This is a gamble taken by anyone planning a controlled experiment.

If the controls succeed, the experiment should permit one to choose with confidence between the following hypotheses: First, that after speciation natural selection has favored ecological diversification with resultingly greatly lowered competition and a greatly increased area of coexistence; and second, that after speciation and reinvasion, natural selection has favored the development in at least one species of mechanisms to increase its competitive ability and thus exclude the congener from all or nearly all of its range. The ability to choose between the two hypotheses would greatly advance our ability to interpret systematic-distributional data from a large array of situations where *post facto* conclusions are all that can be expected.

TABLE 1. The plan and possible outcomes with their interpretations of experimentation in the area where *Plethodon jordani* and *P. glutinosus* overlap broadly in vertical distribution. All controls are described in the text.

MANIPULATIONS	OUTCOME	INTERPRETATION
A. Remove <i>jordani</i> .	a. Disappearance of moved <i>jordani</i> .	Local <i>glutinosus</i> has a competitive adaptation to foreign <i>jordani</i> and local <i>jordani</i> has evolved ecological character displacement.
	1. Replace with <i>jordani</i> from area of narrow overlap.	(I) Combined with a decrease in abundance of <i>glutinosus</i> , means that introduced <i>jordani</i> had evolved a specific competitive mechanism against <i>glutinosus</i> .
	b. Persistence of moved <i>jordani</i> .	(II) Combined with constant <i>glutinosus</i> population, means that local <i>glutinosus</i> has evolved ecological character displacement.
	2. Leave local <i>glutinosus</i> alone.	a. No change in abundance of <i>glutinosus</i> .
B. Remove <i>glutinosus</i> .	b. Increase in abundance of <i>glutinosus</i> .	Means that there was no competition with <i>jordani</i> .
	1. Leave local <i>jordani</i> alone.	a. No change in abundance of <i>jordani</i> .
	b. Increase in abundance of <i>jordani</i> .	Means that there was some competition at a low level.
		Means that there was no competition with <i>glutinosus</i> . (Reciprocal of A 2 a)
		Means that there was some competition with <i>glutinosus</i> at a low level. (Reciprocal of A 2 b)

TABLE 2. The plan and possible outcomes with their interpretations of experimentation in the area where *Plethodon jordani* and *P. glutinosus* have a narrow zone of vertical overlap. All controls are described in the text.

MANIPULATIONS	OUTCOME	INTERPRETATION	
A. Remove <i>jordani</i> .	1. Replace with <i>jordani</i> from area of wide overlap.	a. Disappearance of moved <i>jordani</i> .	Local <i>glutinosus</i> has a specific competitive adaptation to all <i>jordani</i> ; <i>glutinosus</i> should increase in abundance.
		b. Persistence of moved <i>jordani</i> .	(I) If <i>glutinosus</i> increases in abundance or remains stable, indicates that introduced <i>jordani</i> has evolved ecological character displacement with respect to all <i>glutinosus</i> .
	2. Leave local <i>glutinosus</i> alone.	a. No change in abundance of <i>glutinosus</i> .	(II) If <i>glutinosus</i> decreases, indicates specific adaptation by area I <i>glutinosus</i> to coexist with all <i>jordani</i> ; especially strong if combined with A 1 b (II) of Table 1.
		b. Increase in abundance of <i>glutinosus</i> .	Means that original hypothesis of competition was false. Total distribution pattern hard to interpret. Expect other bad results. Habitat disturbed?
B. Remove <i>glutinosus</i> .	1. Leave local <i>jordani</i> alone.	a. No change in abundance of <i>jordani</i> .	Means that original hypothesis of competition was false, especially with A 2 a. (Same interpretation)
		b. Increase in abundance of <i>jordani</i> .	Confirms original hypothesis of competition; <i>jordani</i> should increase more than in B 1 b of Table 1.

SPECIALIZATION AND THE RESULTS OF ECOLOGICAL INTERACTIONS

The evolutionary result of competitive interactions has been the subject of a great deal of speculation, most of it stressing specialization for different resources. This interpretation requires scrutiny, since it implies that differential specialization is a probable result of competition for resources, and the observation of different food habits among coexisting related species has been interpreted as avoidance of competition.

Such an interpretation, to be accepted even provisionally, should require an examination of alternate hypotheses to explain the observation. One such hypothesis that has not been explored adequately, is that specialization carries advantages in efficiency of handling, digesting or metabolizing the food, and that competition need not be invoked at all. Thus, competition is easily shown not to be a necessary condition for the evolution of food specialization. The subject will be pursued to examine the question of the sufficiency of competition as an explanation. If specialization for one kind of food is regarded as a derived state, as either of the above hypotheses assumes, then polyphagy must be regarded as the starting point for any reconstruction. Assuming that such is the case, and that the members of a species are experiencing intraspecific competition for food, an individual of this species which tended to specialize would be at a disadvantage whenever its specialty became scarce, since, in becoming a specialist, it would be expected to lose some ability to handle or digest the remaining kinds of food. The only ways for such a specialist to remain at an advantage would be to begin by being so efficient at obtaining the special food as to overcome the expected periodic scarcity, or else in some way to avoid the expected trade-off in efficiency with regard to other kinds of food. The probability appears to be very low in either case. Thus, for food-limited species polyphagy should be the rule.

With an initially polyphagous species that has a superabundant supply of food, the situation is quite different. Any genotype increasing specialization is likely to be favored because of the benefits of increased efficiency. No penalty is attached to this tendency, because under the terms stated, none of the various kinds of food is ever in short supply. Therefore, contrary to routinely accepted theory, specialization for different foods should be characteristic of species that are not in competition, and the claim is hereby advanced that prior competition is

neither a necessary condition nor a sufficient one to explain the coexistence of closely related species each specializing on a different food.

How is such a claim to be tested? One way would be the laborious one of field experimentation testing for the means of limitation of population size in a large series of related species, some of which were monophagous and some polyphagous. If the former are consistently limited through means other than the supply of their food resources, and the latter show a consistent tendency to be food-limited, the claim would be strongly supported. Rigorous proof of a series of events in evolutionary history is, of course, not possible, and in the present instance, even if the experiments had the expected outcomes, the counterclaim could always be made that the specialists had been released from competition by becoming specialists and therefore would have to be limited in abundance by some other factor.

A *post facto* test of the claim that food specialization implies the absence of prior competition for food can be suggested in the following manner. Among a number of species whose food is well documented, there should be no particular relationship between the degree of specialization and the number of specialized species per species of food. If, on the other hand, specialization represents an evolutionary "escape" from competition for food, the advantage gained should be reflected in a tendency to be the only such species feeding on the food species in question. Thanks to an extensive table by Needham, Frost and Tothill (1928), this test can be made in the case of leaf-mining insect species. There are 435 species of plants that serve as hosts. Of these 289 are fed on by only one species of leaf miner; 82 are fed on by two species, and 64 are fed on by three or more species of leaf miners. On the hypothesis that the distribution of the insect species is by chance among the three groups of plant species, the expected distribution can be calculated by tabulating for each insect species its host plant species with respect to the number of insect species that the host plant supports. Thus, for each specialist, only one plant species will appear in the table; for those feeding on two plant species, both plant species will appear in the table, and the same system continues for insects feeding on three or more species of plants; each plant species will appear separately in the appropriate part of the table. After the removal of those records involving plants determined only to genus, and prorating those appearing more than once in the table, there remain 426 records of the plant species, classified according to

TABLE 3. The number of species of plants attacked by varying numbers of species of leaf-mining insects. The insect species have been separated according to the specificity of their food habits. The figures in the table have been calculated on the assumption of no relationship between the degree of specialization of the insect and the number of species of insects supported by its food plant(s).

Number of species of host plant per species of insect	Number of species of insect per species of host plant		
	1	2	3 or more
1	99.47	28.31	21.87
2	47.21	13.44	10.38
3 or more	136.41	38.83	30.00

TABLE 4. The observed distributions of plant species for comparison with the expected distributions in Table 3.

Number of species of host plant per species of insect	Number of species of insect per species of host plant		
	1	2	3 or more
1	94.00	37.50	18.31
2	48.00	11.00	12.10
3 or more	134.00	38.50	32.95

the number of insect species feeding on them. In the absence of a relationship between specificity of feeding by the insect and the number of insect species supported by the host, these 426 records should be distributed in the ratio 289 : 82 : 64 for each group of insects: those found on one species of plant, those found on two species and those found on three or more species. The expected distributions are given in Table 3.

If specialized species of insects tend to specialize on plant species for which there is little competition, there should be an excess of species in the first column for species with one host, and a corresponding deficiency in the third column for the same row. That such is not the case is shown in the observed distribution (Table 4). Three of the specialists are confined to a plant species that supports them and ten other species of leaf miners; four are confined to a plant species that supports them and eight other species of leaf miners. At the other end of the scale, one species of leaf miner which lives on 37 different plant species is the only species feeding on 19 of these plants. Thus, these data

provide no support for the hypothesis that specialization for specific food items arises as a direct result of interspecific competition, and the data do support the hypothesis that such specialization arises in the presence of ample food of various kinds. The data, incidentally, are also consistent with other kinds of evidence indicating that the terrestrial herbivore trophic level is predator-limited as a whole (Hairston, Smith, and Slobodkin, 1960).

It is now worthwhile to examine the kinds of divergence that would be likely under the selective force of interspecific competition. It is assumed, and will probably be conceded, that competition is likely to be most intense between close relatives, here interpreted as those most recently separated by speciation. It is further assumed that newly separated competing species will be in contiguous but largely nonoverlapping ranges. If the differences between the adjacent places were great enough, the process of adaptation to the separate local conditions would be likely to result in species that were different in many ways, including the acquisition of different kinds of food, even if both species were limited in abundance by their food supplies. Selection might now favor either of two quite different courses: the production of competitive mechanisms specifically against the neighboring species, or further divergence by each species in obtaining food in those parts of the others' range most like its own. The first would sharpen the boundary between the two species, as is the case with *Plethodon jordani* and *P. glutinosus* over parts of their distribution; the second course would be expected to lead to broadly overlapping but different ecological distributions, such as are exemplified by the species of *Desmognathus*. These two courses, as well as the third and noncompetitive course proposed earlier, would have quite different consequences from the standpoint of systematics. The continued highly competitive situation should result in few differences, and it is easy to imagine situations in which hybrids would be at an advantage. The two species of *Plethodon* in the Nantahala Mountains may provide an example. Where the species become differentially adapted to place, it would be expected that many differences would be favored, and that eventually these would become the large differences that characterize higher categories. It would be easy to place *Desmognathus aeneus* and *D. quadramaculatus* in different genera, were it not for the existence of two species intermediate between them in morphology. Finally, in the noncompetitive situation, it might be expected that selection would produce few

differences, but those would be very distinct, and would be such as to put hybrids at a severe disadvantage.

What is being suggested here is that an analysis of the systematic and distributional relationships provides clues to the ecological forces that have been operating on the species in question. In the case of one such situation, there has been proposed a series of experimental tests designed to permit a choice among the ecological and selectional events that led to the present systematic relationships. Without such planned experiments, we are committed at best to accepting "natural experiments," the conditions of which may be unknown to us, and which nearly always lack the elements of controls and of experimental design that promote definitive answers to specific questions. Manipulations will not be possible for all situations, but if the different ecological causes and their systematic effects that I have suggested can be confirmed for a few specific cases, predictive power would be added to the simple analyses to which we are now confined.

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